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BIOLOGICAL BULLETIN

HEREDITY AND ORGANIC SYMMETRY IN ARMADILLO QUADRUPLETS.

I. Modes of Inheritance of Band Anomalies.

H. H. NEWMAN.

Introduction.

Since the winter of 1909, when I first secured and began the study of advanced polyembryonic fetuses of the nine-banded armadillo, I have been struck not only by the striking resemblances among the individuals of a set of quadruplets but also by certain equally striking differences. It was early noted that well defined anomalous arrangements of scutes in the armor bands were sometimes repeated with closely similar detail in two or more fetuses, and were totally absent in others. Occasionally all four fetuses of a set showed a highly localized anomaly, but differed materially in the extent of the irregularity and in its symmetrical relations.

The full significance of these conditions did not dawn upon me, however, until some years later, when a set of quadruplets was obtained in which the band anomaly in question was found to be present not only in all of the four fetuses but in the mother as well. Previous to this time only a few anomalous sets had been studied and these happened to have normal mothers, a circumstance which led to the belief that these characters were not strictly inherited from parents but were merely predetermined early in embryonic life before the separation of the four embryos from the originally single embryonic vesicle. The finding of one unequivocal case of the direct inheritance from the mother of the anomalous character stimulated a new interest in the problem and made it necessary to collect a large amount of new

data. Accordingly in the winter of 1911 I journeyed from Chicago to Texas and spent about a month in the armadillo country collecting material, obtaining nearly two hundred advanced polyembryonic sets together with the armor of the mothers.

A study of this material by my students and myself has brought to light a situation so interesting, but withal so intricately complex, that I almost despair of being able to render an intelligible account of it. Yet I cannot but be impressed with the uniqueness of the data and with the fact that it contains clews, afforded by no other material, as to methods of attacking some of the problems of the mechanics of hereditary transmission and of the development of organic symmetry.

In presenting the results of the study of the heredity of band and scute anomalies I have found that the problems of heredity, and that of the symmetrical distribution of these inherited characters among the quadruplet embryos, are inseparably parts of a larger problem that has to do with the mechanics of organic symmetry. When, for example, it is found that a bilateral anomaly in a mother is inherited unilaterally in the various offspring and appears in reversed symmetrical relations in twins, we have something more than a case of simple inheritance. When again we find a unilateral anomaly in one pair appearing bilaterally without reversed symmetry in the opposite pair we see the problem in a more complex form. When, still further, we note that an anomaly of a single scute in the mother is inherited as such in some of the offspring and as a whole series of anomalous scutes (a band anomaly) in others, we begin to suspect that the problem is too intricate for any simple solution and that only in certain of its aspects is it likely to yield to analysis. Yet it is our duty to carry the analysis as far as our data allows.

That the circumstance of polyembryony vastly complicates the already sufficiently complex problems of heredity can scarcely be denied, but it is confidently hoped that the new relations introduced by this unique type of development may throw light from a different angle upon certain phases of heredity that are now quite obscure.

Before the reader can appreciate the significance of the data on heredity and organic symmetry, it will be necessary for him to be made familiar with the character of the material and its specific frequency and distribution.

Material and Methods of Study and Presentation.

The material for this investigation consists of nearly two hundred sets of quadruplet fetuses in advanced stages, showing the definitive arrangement and number of scutes in the armor. In every case the shell of the mother was obtained and preserved so that there is on hand complete data on uniparental inheritance of armor characters. The fetuses and the respective mothers make up a collection of nearly one thousand individuals, which is unquestionably a representative sample of the species.

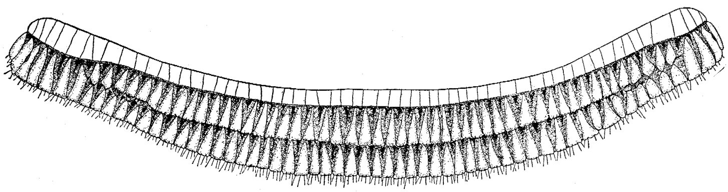
Counts of scutes and records of anomalies have been made independently by at least two workers and all differences or discrepancies have thus been checked and corrected, so that the probability of error and personal bias have been eliminated.

Since the anomalies here dealt with are rare, occurring in only about three per cent. of individuals, I have made an examination of the preserved armor of 1,800 adults that formed the stock of a single dealer. This was done in order to determine the limits of diversity and the specific distribution of the anomalies. A complete record of all these anomalies has been made in the form of a pictorial diagram in Table *A*, 1, 2 and 3.

In order that the reader may understand the nature of the anomalies it will be necessary to give a brief statement of the normal relations of armor units. The primary unit of the armor is a threefold complex consisting of a bony plate, covered by a primary epidermal scale of scute, and a group of hairs that are imbedded in the bony plate and perforate the scute. For convenience this complex is called a "scute." In young fetuses the outline of the epidermal scute is all that can be seen; but this visible unit stands for the whole complex. These scutes or armor units of the carapace are arranged differently in the three main subdivisions of the armor, the pectoral, banded and pelvic shields. In the pectoral and pelvic regions the bony plates are arranged like tiles and form a rigid immovable shield. Naturally

the primary scutes are arranged in more or less regular transverse rows, but these rows seldom run straight across the shield. Instead it is commoner for a row that starts single on the margin to become double for some distance where the bulge of the shell is greatest, then to be single again toward the middle. Again a row may start double laterally and be single for a short distance toward the middle. Irregularities in scute rows are commonest near the posterior border of the pectoral shield next to the banded region.

In the banded region the arrangement of scutes is quite different. The bony plates are elongated antero-posteriorly to form rows of units, in general appearance somewhat like the keyboard of a piano. The posterior margin of the first band is free from and slips over the anterior margin of the second, an arrangement that lends flexibility to the armor. The second band bears a similar relation to the third and so throughout the nine movable bands. Each bony plate is accompanied by and partially covered by an elongated, wedge-shaped primary scute. Figs. 1 and 3 represent two bands removed whole from the armor. The typical band, however, is composed of an even array of scutes arranged in a single row from margin to margin. Only one third of one per cent. of the 16,200 bands examined are in any way irregular in the arrangement of the armor units. The rare exceptions, however, are of especial interest and constitute the anomalies that are the subject of the present study. These peculiar bands belong for the most part to the types, the details of which are shown in Figs. 1, 3 and 5. They consist of bands that are partly single and partly double. In Fig. 1 is seen a very common type of bilateral anomaly in which a few scutes on each margin constitute the single part of the band, while the main central region is double. In Fig. 3 we see an equally common condition in which the double part of the band is confined to a number of scutes starting at some distance from the margins but stopping short of the middle portions of the band. Similar conditions of greater or less extent are found unilaterally as frequently as bilaterally. Now these irregular bands are in no sense abnormalities or products of injury, but are of the same nature exactly as are the irregulari-



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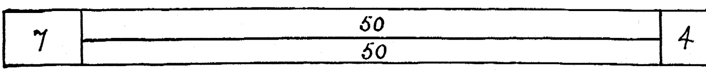

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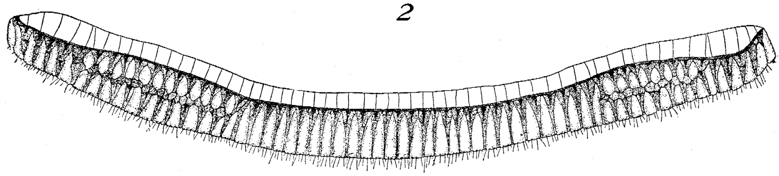

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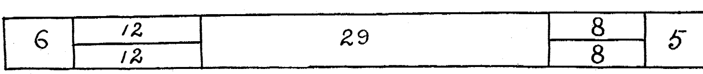

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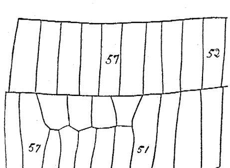

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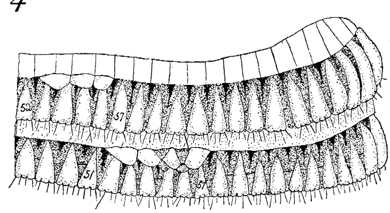

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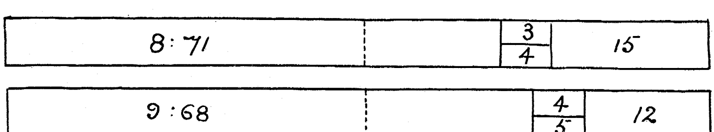

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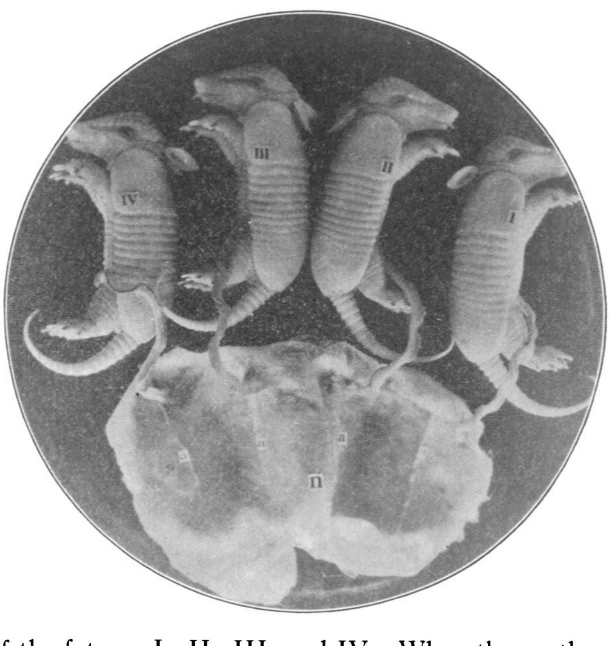
ties of scute rows in the adjacent pectoral shield, where regularity is rare and irregularity the typical condition. In about three per cent. of individuals the irregular conditions typical for the posterior part of the pectoral shield invade the adjacent parts of the banded region. That this is the correct interpretation of the anomalies in the banded region is evidenced by the fact that out of 84 band anomalies recorded for this study 73 occur in the first band, which is contiguous to the pectoral shield. Of the remaining eleven cases 7 occur in band 2, 1 in band 3 and 1 in band 8, which is near the other irregular region, viz., the pelvic shield. Irregularities never occur in the middle bands of the carapace, which are farthest from the irregular pectoral and pelvic shields. Another way of interpreting the facts is to look upon the arrangement of scutes in the banded region as due to mechanical adjustments of the primordia of armor elements to flexures during embryonic development. Typically the banding confines itself to the abdominal parts of the armor but occasionally comes in a little farther forward or a little farther back and thus includes parts of the pectoral and pelvic carapace with the typical peculiarities of scute arrangements of these regions. As a result we have these anomalous cases in which the first or second band has the characteristics, doubling, etc., of the pectoral region, and the posterior bands have similarly the characteristics of the pelvic region.

An irregularity in a given band of the banded region may involve as few as two or even one scute. Such an irregularity may consist of a single scute or two in an otherwise double band or a double scute or two in a band otherwise single. The latter situation is much the commonest of all anomalies studied. Sometimes the anomaly manifests itself by a more or less complete longitudinal or diagonal splitting of a single acute. Such conditions are to be dealt with separately as there is a considerable mass of interesting data on the inheritance and distribution of these anomalous double scutes. It is impossible, however, to deal with the inheritance of anomalous band conditions without discovering the intimate genetic connection that exists between band and scute anomalies, for sometimes a scute anomaly in a parent reappears as a band anomaly in offspring and vice versa.

After many experiments in tabulating the occurrence of band and scute anomalies I have adopted a simple pictorial scheme which will readily explain itself on examination of the diagrammatic Figs. 2, 4 and 7 which are simplified representations of the scute conditions shown in Figs. 1, 3 and 5 respectively. The numbers of scutes in both double and single regions are represented by arabic numerals and the number of the band is indicated sometimes, as in Table *A*, 1, 2 and 3, by the abbreviation Bd. 1 or Bd. 2 just above the margin of each band, and sometimes as in table B by a single arabic numeral followed by a colon and the total number of scutes in the band. When the quadruplet fetuses and the mother are dealt with, the number of the set is indicated as A.101 ♀ or K.40♂, indicating at the same time the sex of the litter; the bands of the mother are labeled M and



those of the fetuses I., II., III. and IV. When the mother or any fetus is not tabulated the inference is that no anomaly is present in the omitted individuals. Other schemes of tabulation, such as the circular figures and those showing double scutes will be explained in the proper place.

Specific Distribution and Frequency of Band Anomalies.

Little need be added to the data given in Table *A*, 1, 2, 3, which shows the anomalies found in 1,800 adult specimens. On previous occasions I have made records of over 1,000 other specimens and have failed to find any other types of diversity than those shown in this table. So it may be considered as established that we have before us in this collection an adequate representation of the diversity of band anomalies and their distribution among the various bands. Although no two irregular bands in unrelated individuals are just alike there are certain well-defined classes of anomaly such as the bilateral (symmetrical or asymmetrical) and the unilateral. There are types single on the margins and double in the middle; there are types double at the margin and single in the middle; and there are mixed types.

Specimens 1–14 show various types of anomaly in which the bands are single at the margin with bilateral regions of doubling. Specimens 15 to 35 show unilateral expressions of the same types of anomaly. Specimens 36–42 show various mixed types, which are perhaps reversals of anomalies of the two sides of the individuals. Fig. 42 is an especially interesting case of such a reversal of symmetry, for the right and left halves of the band are duplicates but are not mirror-image effects. They bear the same relation to each other as the reversed finger prints found occasionally on the right and left index fingers of human duplicate twins, as shown by Wilder.

Some of the cases of exact bilateral symmetry, such as those in specimens 5, 7 and 36 are very significant, and there are all degrees of inexact bilateral duplication of anomalies ranging from specimens 12, 4, 8, 11, 14 down to specimens 13, 10, 9, 6, etc.

It must not be forgotten that there are no two anomalies alike in nearly three thousand specimens taken at random. When, therefore, we find, as we soon shall, exact duplicate anomalies in two or more fetuses in a set we shall not be able to explain them as coincidences.

Having made clear the nature of the anomalies and their diversity and distribution in the species, we are now in a position to examine the data on the inheritance of these characters.

TABLE A1.

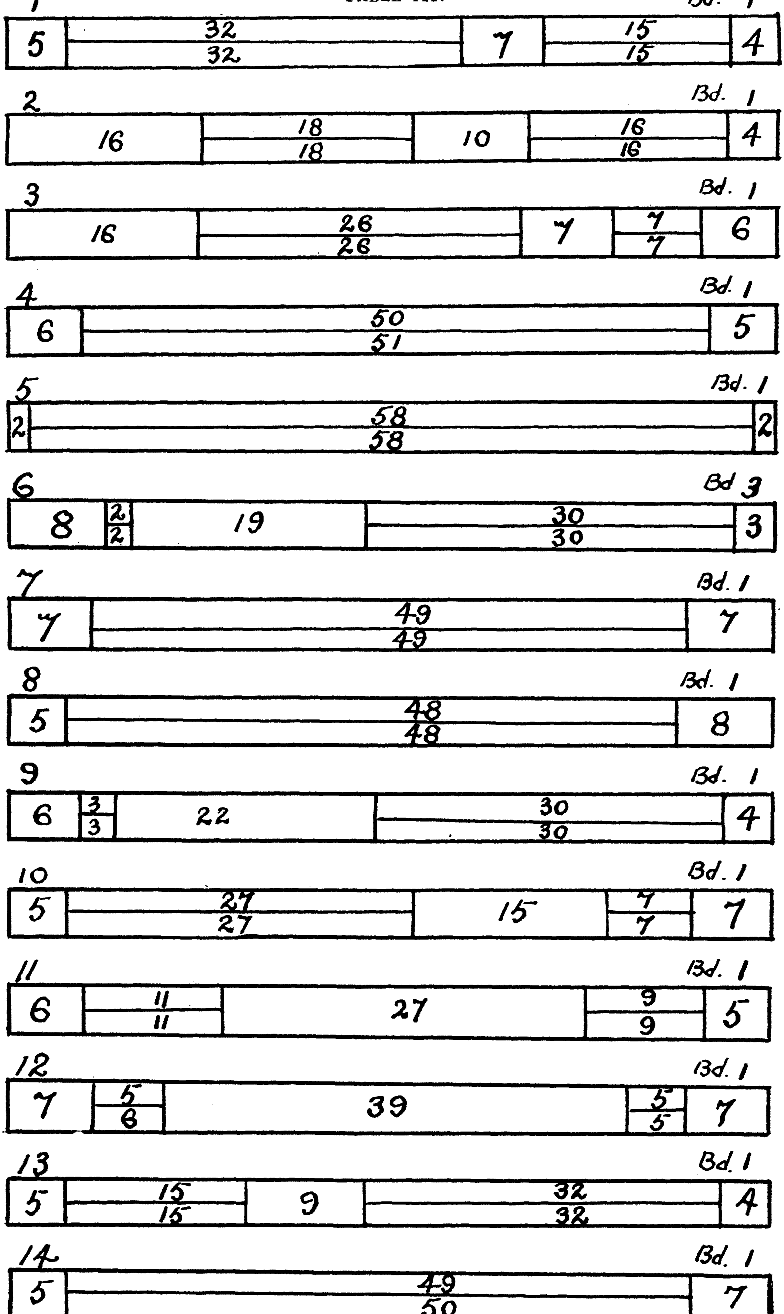

1 Bd. 1
5 | 32/32 | 7 | 15/15 | 4
2 Bd. 1
16 | 18/18 | 10 | 16/16 | 4
3 Bd. 1
16 | 26/26 | 7 | 7/7 | 6
4 Bd. 1
6 | 50/51 | 5
5 Bd. 1
2 | 58/58 | 2
6 Bd 3
8 | 2/2 | 19 | 30/30 | 3
7 Bd. 1
7 | 49/49 | 7
8 Bd. 1
5 | 48/48 | 8
9 Bd. 1
6 | 3/3 | 22 | 30/30 | 4
10 Bd. 1
5 | 27/27 | 15 | 7/7 | 7
11 Bd. 1
6 | 11/11 | 27 | 9/9 | 5
12 Bd. 1
7 | 5/6 | 39 | 5/5 | 7
13 Bd. 1
5 | 15/15 | 9 | 32/32 | 4
14 Bd. 1
5 | 49/50 | 7

TABLE A2.

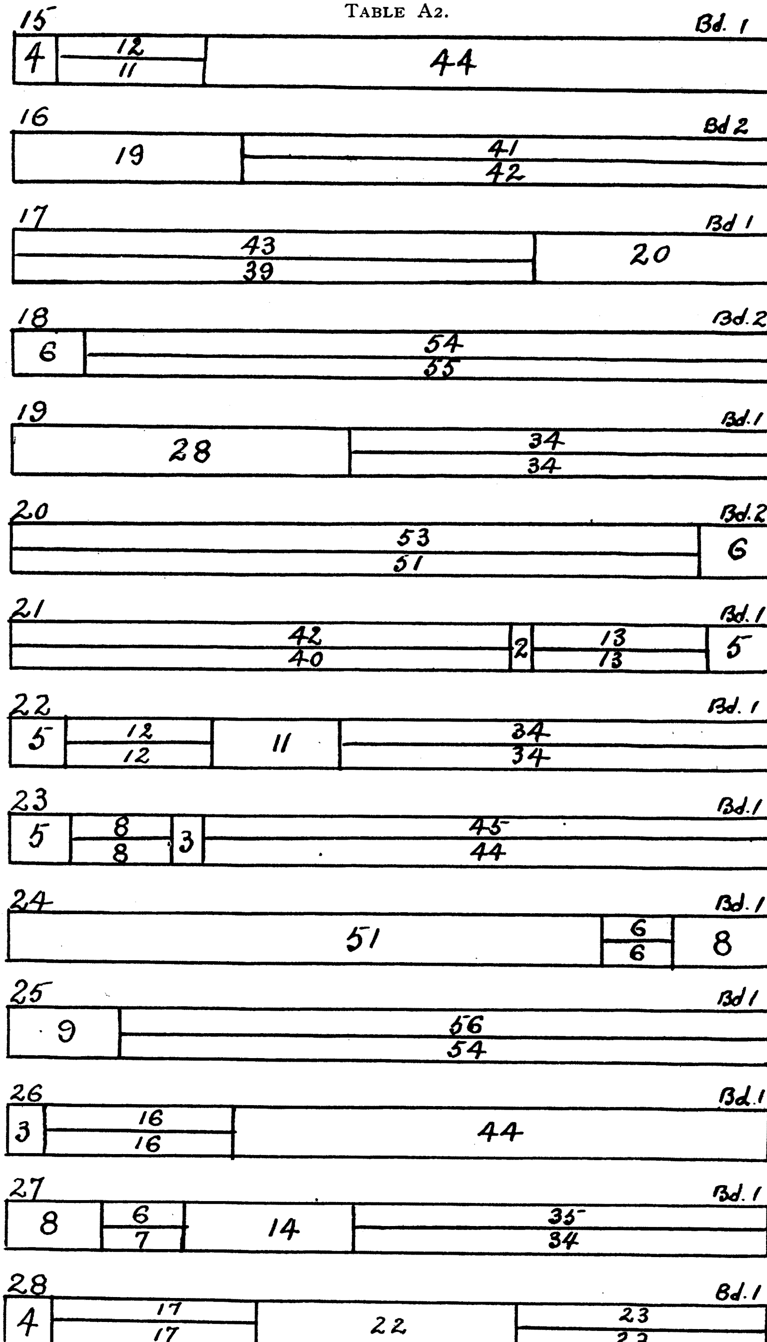
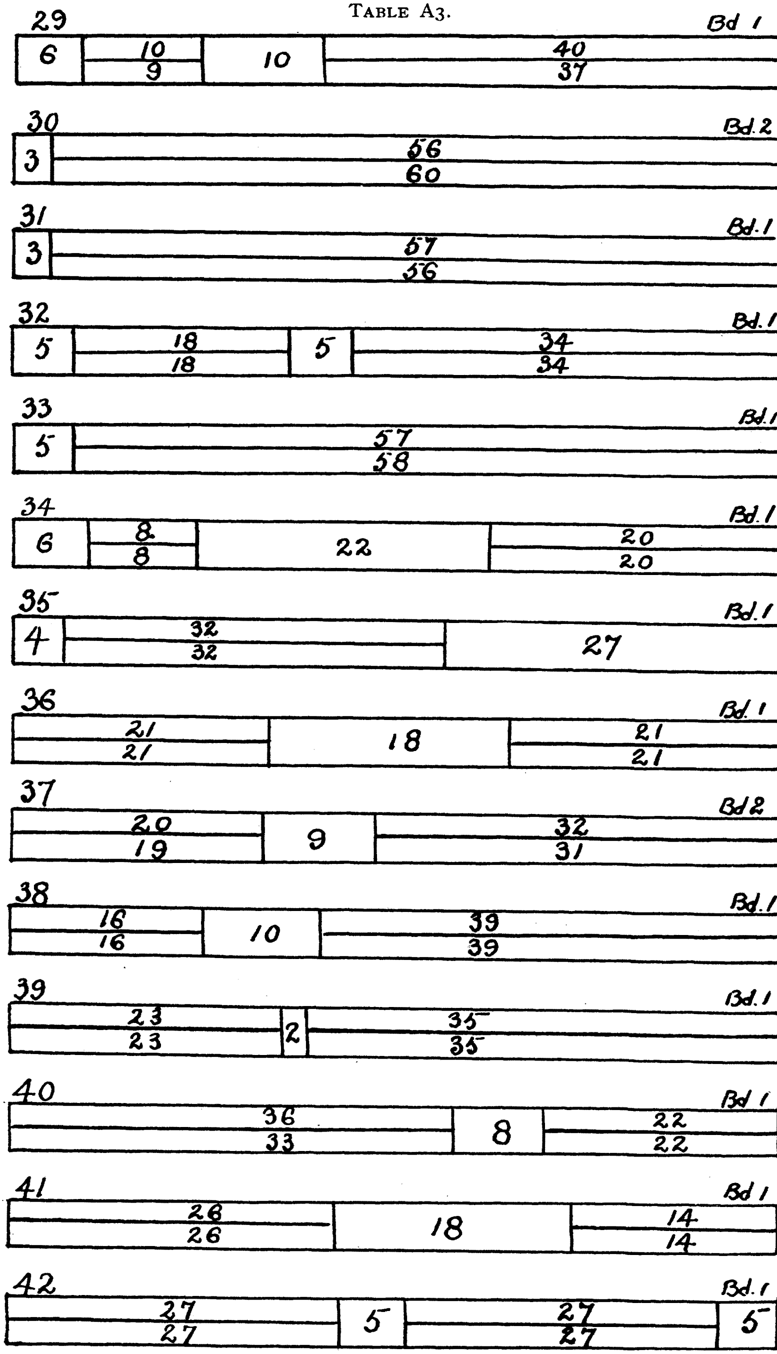

15
Bd. 1
4
12
11
44
16
Bd 2
19
41
42
17
Bd 1
43
39
20
18
Bd. 2
6
54
55
19
Bd. 1
28
34
34
20
Bd. 2
53
51
6
21
Bd. 1
42
40
2
13
13
5
22
Bd. 1
5
12
12
11
34
34
23
Bd. 1
5
8
8
3
45
44
24
Bd. 1
51
6
6
8
25
Bd 1
9
56
54
26
Bd. 1
3
16
16
44
27
Bd. 1
8
6
7
14
35
34
28
Bd. 1
4
17
17
22
23
23

TABLE A3.


29
Bd 1
6
10
9
10
40
37
30
Bd. 2
3
56
60
31
Bd. 1
3
57
56
32
Bd. 1
5
18
18
5
34
34
33
Bd. 1
5
57
58
34
Bd. 1
6
8
8
22
20
20
35
Bd. 1
4
32
32
27
36
Bd. 1
21
21
18
21
21
37
Bd 2
20
19
9
32
31
38
Bd. 1
16
16
10
39
39
39
Bd. 1
23
23
2
35
35
40
Bd 1
36
33
8
22
22
41
Bd 1
26
26
18
14
14
42
Bd. 1
27
27
5
27
27
5

The Inheritance and Distribution of Band Anomalies.

After a study of over 150 of the most advanced sets of quadruplets in my collection I am convinced that both band and scute anomalies are strongly inherited. In every case in which a mother exhibits a band or a scute anomaly, a related anomaly is found in one or more of the offspring. If the character were not inherited as a dominant, one would expect some exceptions to this rule, but none have been found. When, therefore, we find an equal number of offspring of normal mothers exhibiting anomalies of the same sort we are justified in concluding that the characters represent a heritage from the unknown fathers. This assumption is farther justified by the finding that the characters in question are neither sex-limited nor sex-linked.

For our purposes, then, the data here published are adequate in that a study of uniparental inheritance reveals fully the modes of inheritance that obtain for band and scute anomalies. Whatever genetic relations are found to hold between mothers and offspring would doubtless hold for fathers and offspring. The only unfortunate complication that is encountered is in connection with a small per cent. of cases in which both fathers and mothers possess anomalies. A few sets of fetuses are obviously of this dual anomalous parentage, and we can, by knowing the maternal anomaly, make a well-founded conjecture as to the probable nature of the anomaly in the unknown father.

Whether or not I am justified in assuming that the study of maternal inheritance reveals the essential facts concerning the inheritance of the characters in question, can be settled only by breeding and, as has been pointed out in extenso in an earlier paper (Newman, '13), breeding experiments with the armadillo are at present totally impracticable. Consequently, we are forced to rely upon a study of inheritance from one parent, the mother.

The nature of the anomalies is such that I have been unable to devise any really convenient method for tabulating the facts that must be known about them. It seems necessary to consider each case of inheritance separately, and this may be done without undue prolixity because the cases are not numerous. The pictorial method appears to be well adapted for the data, but it

would be too tedious a task to draw each anomaly in detail after the fashion of Figs. 1 and 3. Instead I shall use the diagrammatic form seen in Figs. 2 and 4, which give all the necessary information. The best method I have been able to devise for showing the symmetrical or asymmetrical relations of the anomalies and their distribution among the quadruplet fetuses of a set is that shown in Figs. 9–16, in which the anomalous bands are placed as though within the embryonic vesicle. The reader must remember that the structures studied are integumentary units, that the embryonic vesicle is so inverted that the ectoderm forms the inner lining and the endoderm is on the exterior.

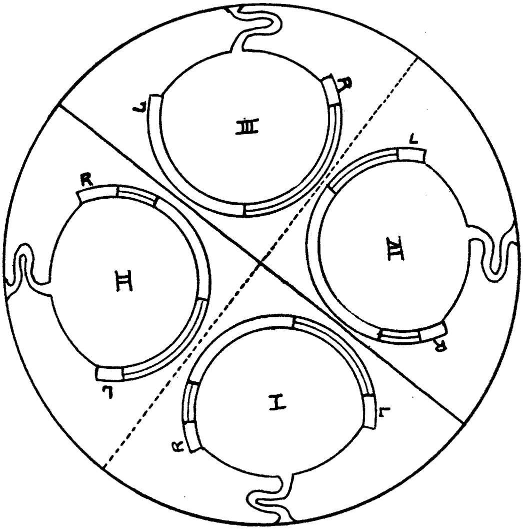
The diagram (Fig. 8) shows the relative positions of the band anomalies of the fetuses in set 87 (Fig. 9). Here we have an equatorial cross section of an advanced vesicle with the body of each fetus severed at the first armor band where the anomaly occurs. The ventral surfaces face outward and are attached by their respective umbilical cords to the placental portion of the vesicle. The dorsal aspects are turned inward. Right and left sides of each fetus are indicated. The reader must imagine himself in the center of the vesicle facing outward toward each fetus. In order to simplify this type of diagram, I have found it best to ignore all structures but the band in question and to represent the latter as though straightened out against the periphery. The reader will understand the adopted form of diagram after a comparison of Fig. 8, which represents nearly the actual relations present in set 87, and Fig. 9, which is a diagram of the same set showing only the bands that are of interest in this study. In both figures the solid quadrant line divides the twins I. and II. from twins III. and IV. and the dotted line separates twin individuals, I. from II. and III. from IV. In the actual vesicle these quadrant lines are occupied by amniotic partitions that hermetically isolate each fetus from the others. When the anomaly is found in the mother also the material condition is indicated in a straight band diagram beside or beneath the circle showing the offspring. When any individual shows an anomaly in more than one band, the more anterior anomaly is shown in the circle and the more posterior anomaly in a concentric sector outside of the circle, as in Fig. 9.

Of the twenty-six sets of fetuses one or more individuals of each of which show band anomalies, twelve came from mothers that also showed either band or acute anomalies, and fourteen came from mothers that showed no anomaly. Presumably the anomaly has been inherited from the father in these fourteen cases.

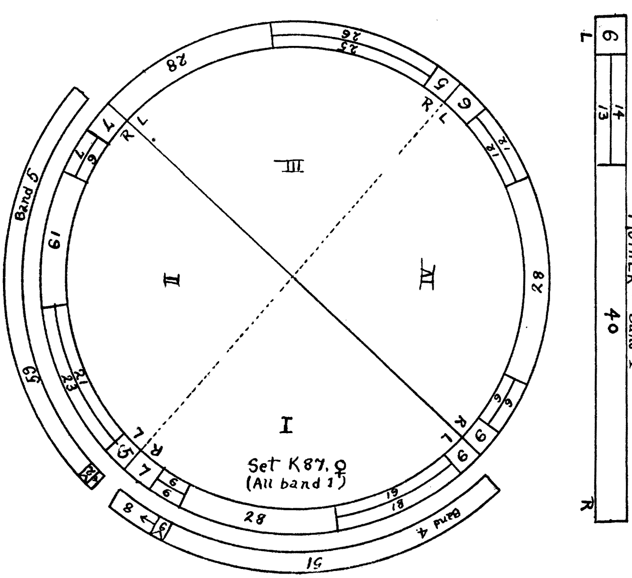
Of the twenty-six sets showing band anomalies exactly half are male and half female, which demonstrates that the characters dealt with have no sex-limitation or sex-linkage. Males and females inherit equally strongly from the mothers, for of the twelve sets of offspring in which the mother also shows an anomaly, five are of the female and seven of the male sex. In the case of four sets with anomalous mothers and similarly in four sets with normal mothers, I shall follow the plan of placing a circular diagram and the verbal description and analyses close together in the text. The remaining sets are tabulated in somewhat more compact form and placed at the end of the paper. Those in Table *B* are the eight remaining sets that have the anomaly in both mother and one or more offspring; those in Table *C* are the remaining ten sets with band anomaly in one or more fetuses but with normal mothers. Each set is placed in a separate block and labeled at the upper left-hand corner, with the number of the set and the sex of the young, as *C* 29 ♂. The number of the band showing the anomaly is indicated in two ways, as bd. 1 or bd. 2 placed next to or on the band, or by a number placed on the band followed by a colon and the total number of scutes in the band, as 7: 65, meaning band 7 having a total of 65 scutes. In bands more or less broken by doubling the number of scutes in each part is indicated. In the case of short series of double scutes or one double scute, the number placed on the element, together with the arrow, indicates the numerical position of the element from either margin, or from the middle, which is indicated by a dotted line.

Set K. 87, ♀ (Figs. 8 and 9).

This set shows more certainly than any other the direct inheritance of a material band anomaly by all of the offspring. In the mother the anomaly consists of a unilateral local doubling


R
L
III
L
II
R
II
L
R
I
L
R

8


III
II
II
I
Set K87, ♀
(All band 1)
Band 5
Band 4
MOTHER - Band 1
40

9

of band 1, confined to the left half of the band and almost identical with the left half of the band pictured in Fig. 3. The band begins on the left lateral margin with six single scutes, is then double for 14–13 scutes and single for the remainder of the series. No other anomalies are exhibited by the mother. Fetuses I., II. and IV. show similar anomalies of band 1, but they are unequally bilateral in their expression (like Fig. 3), all three showing more scutes double on the left than on the right. Fetuses I. and II. are strikingly similar in the distribution of single and double scutes and show no reversal of symmetry. Fetus IV. is the most nearly bilaterally symmetrical in the disposition of its scutes. Fetus III. is unilateral like the mother, but shows a reversal of symmetry in that the doubling is confined to the right side. The symmetry of fetus III. is also a reversal of that of fetuses I., II. and IV., which show a preponderance of doubling on the left side. In addition to the anomalies referred to, fetuses I. and II. show scute anomalies of bands 4 and 5 respectively that do not appear to be traceable to the mother and have presumably come from the father. This is one of the rare sets in which it is probable that anomalies came from both sides of the family. The double scutes of I. and II. are in a reversed symmetry to each other, being near the right in fetus I. and near the left in fetus II.

Set K. 30, ♀ *(Fig. 10).*

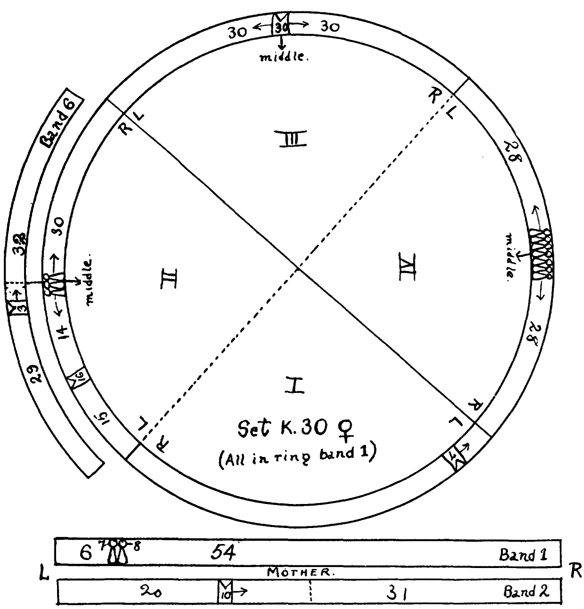
This set is of importance in that it deals with short rows of double scutes ranging from 2 to 7 elements and serves to emphasize the genetic connection between plate and scute anomalies.

The mother has in band 1 in the positions 7 and 8 from the left two adjacent double scutes forming a band anomaly of minimal size but of the same character as the short double regions of the band pictured in Fig. 5. If only one scute had been double-tiered, we would have called it a "scute" anomaly instead of a "band" anomaly. There is also in the mother an independent double scute situated 10 places to the left of the middle of band 2.

Fetus I. has a double scute in band 1 in exactly the position of the first of the two double scutes of the mother. This seems

to indicate that a double scute and an incipient double band are genetically equivalent.

Fetus II. has in the exact middle of band 1 a short series of three double scutes like the two which are near the left margin of the mother; and in the same band, midway between the middle and left band margin, one double scute. In band 6 of the same fetus there occurs at a point three scutes to the left of the middle another double scute like that in band 1. Note that all asymmetrical anomalies are on the left side as in the mother.



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Fetus III. has one double scute in the exact middle of band 1, or in a position identical with the short double band in fetus II.

Fetus IV. has a double region of 7–7 scutes in the exact middle of band 1. This doubling is simply a more pronounced case of the doubling shown in the mother as in fetuses II. and III.

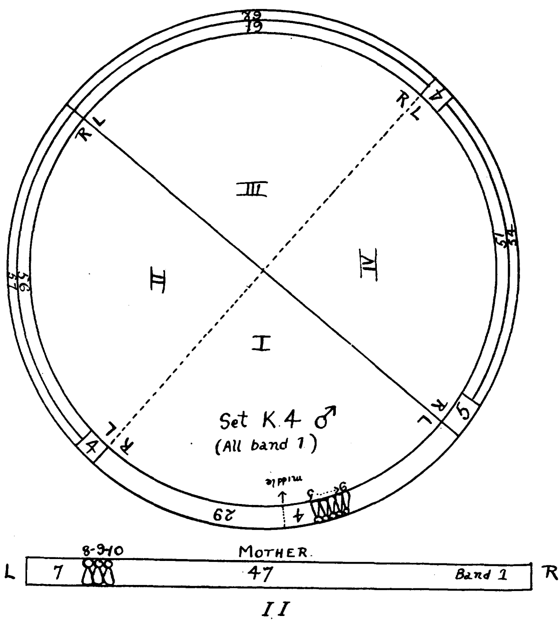
The points of interest illustrated by this set are:

1. In mother and offspring the unilateral symmetry is the same throughout except that there is a tendency for the anomaly to shift to the center of the band. This shifting of lateral anomalies to the center is a peculiar type of symmetry reversal in which the central and lateral portions of each half band become

reversed. That this is the correct interpretation of the situation is amply shown by many cases shown subsequently.

2. There occur several examples of the reduplication of a single inherited unit, sometimes involving a single band, sometimes two or more. Doubtless the anomalies of band 1 and band 2 in the mother represent a merely reversed reduplication of the same inheritance unit. Similarly in fetus II. the series of three double scutes in the middle of band 1, the double scute near the middle of band 6 and the scute in the middle of the left half of band 1 are varied manifestations of the same anomaly.

3. There is more extensive doubling in the two primary bud individuals II. and IV. than in the two secondary bud individuals I. and III.



Set K. 4, ♂ *(Fig. 11).*

The mother has a short series of 3 double scutes in positions 8, 9 and 10 from the left.

Fetus I. has a series of 5 double scutes occupying positions 5, 6, 7, 8 and 9 from the middle of the band.

Fetus II. has on the left 4 single scutes, and the rest of the

band, beginning in position 5, is double. The symmetry is that of the mother, but the doubling involves most of the band. The symmetry is a half-band reversal of that in fetus I. in that the doubling begins 5 scutes from the left margin instead of 5 scutes from the middle.

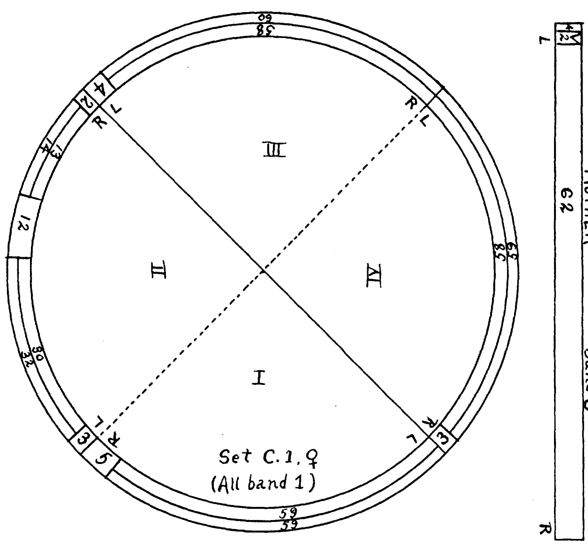
Fetus III. has either no anomaly at all or else has the entire band doubled. It is difficult to decide as to these alternatives.

Fetus IV. has the anomaly bilaterally symmetrically. One might claim that the anomaly that should have appeared on fetus III. has been transferred to fetus IV. so that the latter has a double dose of it.

Set C. 1, ♀ (Fig. 12).

The mother has in band 3 in the second position from the left a double scute.

Fetus I. has an extensive doubling beginning 5 scutes from the



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right-hand margin of band 1. Thus the symmetry of the mother is reversed.

Fetus II. has an extensive unequal bilateral doubling beginning after two scutes on the right and three on the left, continuing to the middle on the left and for 13–14 scutes on the right.

Fetus III. has the doubling of band 1, beginning 4 scutes from the left. The symmetry is the same as that of the mother, but a reversal of that of the opposite individual, fetus I. Fetus III. is therefore a mirror-image of fetus I.

Fetus IV. has the anomaly beginning after 3 single scutes from the right margin of band 1. The symmetry is a reversal of that seen in its twin partner, fetus III., and of that of the mother, so that III. and IV. are mirror-images of each other.

This set shows clearly that a double scute is genetically equivalent to a double band. It is seldom that one finds a set showing such extensive reversals of symmetry.

Set C. 29, ♂ (Table B1).

This set is the complement of set C. 1, in that the mother has an extensive band doubling and the offspring inherit it in the form of scute doubling.

The mother has in band 1 beginning 4 scutes from the left a doubling extending to the right margin.

Fetus II. has in band 7 the second scute from the right double.

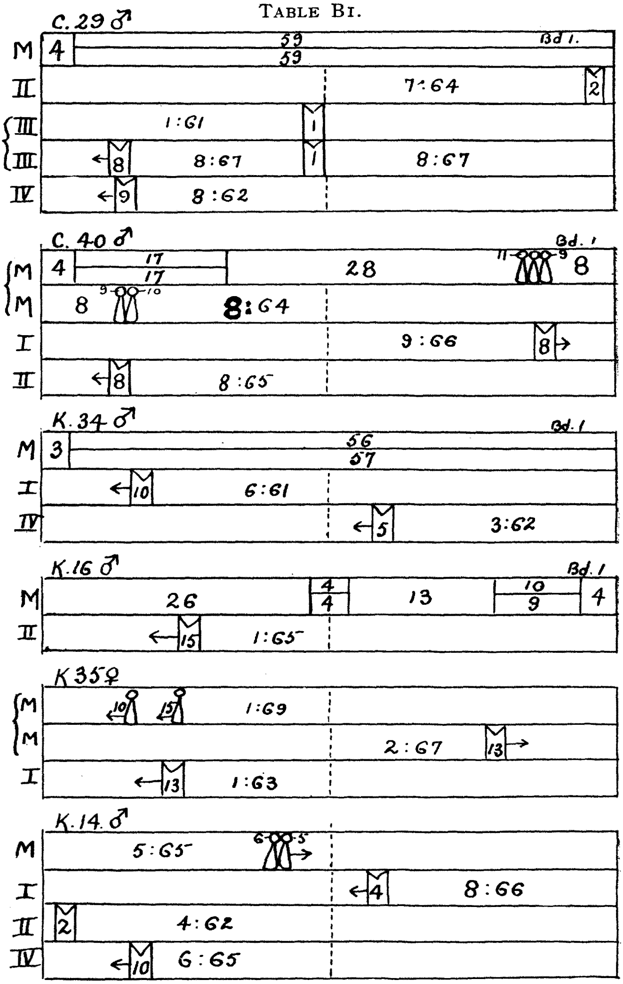
Fetus III. has in band 1 and in band 8 just to the left of the middle a double scute, and in addition a double scute 8 scutes from the left in band 8.

Fetus IV. has in band 3 a double scute in the ninth position from the left.

This set illustrates an extreme case of positional shifting of a genetic character. There can be no question of the relationship between the two scutes of fetus III., occurring in band 1 and band 8 just to the left of the middle. This is a case of reduplication of inheritance unit along the antero-posterior axis. Similarly scute 8 in band 8 of fetus III. and scute 9 in band 3 of fetus IV., are expressions at different levels of the antero-posterian axis of the same genetic unit.

The double element next to the right-hand margin of band 7 in fetus II. is certainly the same genetic unit as the element next to the middle of band 8 of fetus III., but with a reversal of symmetry. Thus by the application of the principle of symmetry reversals and reduplications down the primary axis we can connect up even such apparently unrelated units as these.

TABLE B1.



Set C. 40 ♂ (*Table B1.*)

Here the same type of inheritance is seen as in set C. 29, but the genetic relations are much clearer, and involve no strain upon one's credulity.

The mother has in band 1 a bilateral doubling, beginning on the left after four single scutes and extending in a series of 17-17 double scutes and beginning on the right after 8 single scutes and continuing for a short series of 3-3 double scutes. In addition we find in band 8 a doubling strikingly like that of the right side

of band 1, but reversed to the left and involving only 2 scutes. This is another case of reduplication in anterior and posterior parts of the banded region, but there is also in this case a symmetric reversal.

Fetus I. has in band 9 in position 8 from the right a double scute. This is evidently the genetic equivalent of the two double scutes in band 8 of the mother, but the symmetry is reversed.

Fetus II. has in band 8, 8 scutes from the right, a double scute which is doubtless the reversal or mirror-image of that in its twin partner, fetus I.

Set K. 34, ♂ (Table B1).

In this set the genetic relations are quite obscure.

The mother has in band 1, beginning after 3 single scutes on the left a doubling of the rest of the band.

Fetus I. has in position 10 from the left margin of band 6 a double scute.

Fetus IV. has in position 5 to the right of the middle of band 3 a double scute.

Set K. 16 ♂ (Table B1).

The mother shows a right lateral and a median doubling of band 1.

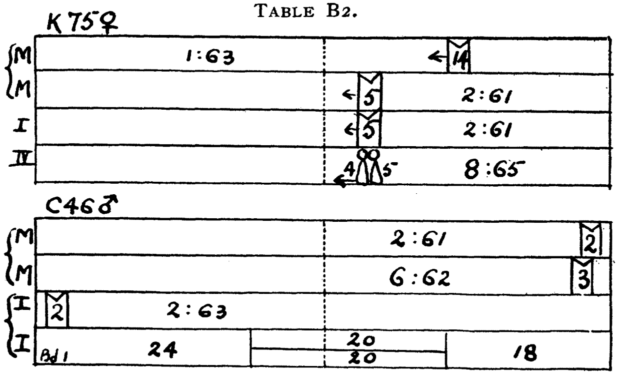
Fetus II. has one double scute in band 1, situated in the middle of the left side of band 1, another case of centro-lateral symmetry reversal.

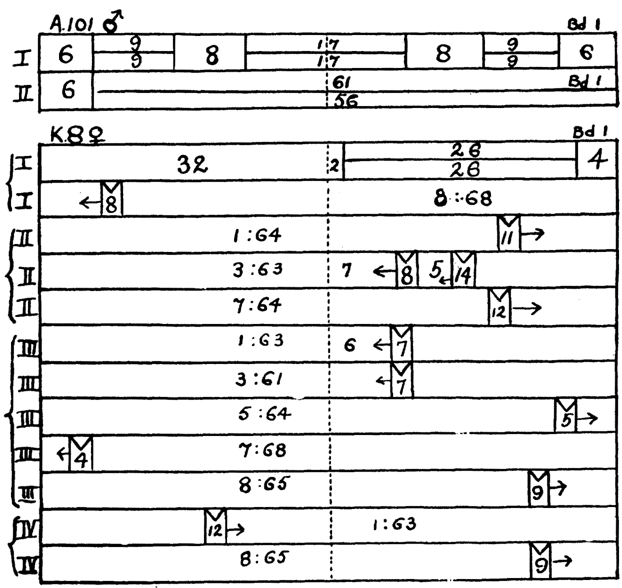
Set K. 35, ♀ (Table B1).

The mother has a rather unusual anomaly in the form of two "split" scutes separated by several single scutes, occurring in band 1, in places 10 and 15 respectively from the left-hand margin. In band 2 we find the bilateral equivalent of these elements in the form of one double scute situated in position 13 from the right.

Fetus I. is the only one of the offspring to inherit the maternal anomaly. There is in band 1 a double scute situated 13 places from the left in the reverse position of that seen in band 2 of the mother. The genetic relations here are quite clear, but why should only one out of four offspring show an inherited character?

TABLE B2.





Set K. 14 ♂ (Table B1).

The mother has an incipient double band of two scutes in positions 5 and 6 to the left of the middle of band 5.

Fetus I. has a double scute in position 4 to the right of the middle of band 8. This shows reversed symmetry and a shifting down the primary axis of the genetic unit inherited from the mother.

Fetus II. has a double scute in position 2 from the left-hand margin of band 3. This is evidently a reversal of the conditions seen in the mother and is also a complex reversal, with shifted position on the primary axis, of the condition seen in its twin partner, fetus I.

Fetus IV. has a double scute in band 6, situated with reference to the middle of the left half band in about the same relation as is the peculiarity of the mother with reference to the middle of the whole band. In other words it is 5 scutes to the left of the middle of the left half of band 6, while that of the mother is situated 5 scutes to the left of the middle of band 5. Considering the rarity of anomalies of any sort in the bands 3, 4, 5 and 6, there can be no doubt of the genetic identity of these elements. Granting this the interpretation offered is not forced.

Set K. 75, ♀ (Table B2).

Here the mother has two double scutes, one near the middle of the right half of band 1 and another to the right of the middle of band 2.

Fetus I. has a double scute in band 2 identical in position with one of those of the mother.

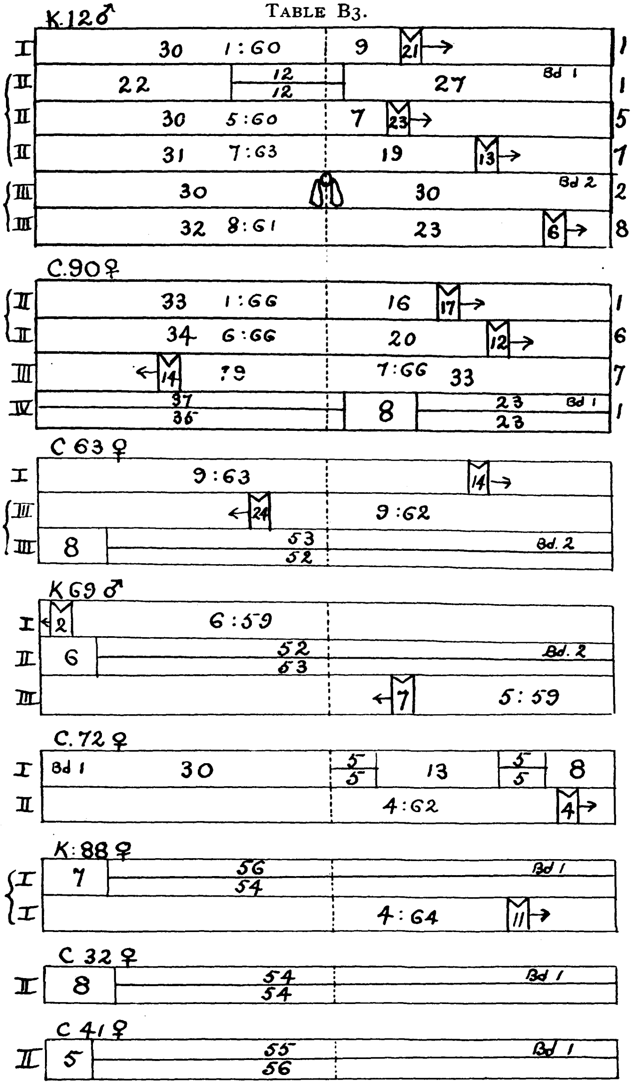
Fetus IV. has in band 8, in a position with reference to the middle identical with one of those of the mother and that of fetus I., an incipient band doubling of 2 scutes. This is another example of the shifting of an anterior element to a position further down the primary axis. It also emphasizes the genetic identity of band and scute doublings.

Set C. 46, ♂ (Table B2).

The mother shows a reduplicated double scute anomaly in bands 2 and 6 in positions 2 and 3 respectively from the right-hand margin.

Fetus I. shows in band 2 an exactly reversed mirror-image reversal of the anomaly in band 2 of the mother and in addition an extensive doubling in the middle of band 1. This illustrates three points; (*a*) reduplication down the primary axis, (*b*) the genetic relation between scute and band doubling, (*c*) the half-band type of reversal of symmetry.

TABLE B3.



It should be noted by way of summary that in all cases in which the mother has a band anomaly, one or more offspring of a set have usually a similar band anomaly; but sometimes a scute anomaly is found to be the expression in the offspring of a maternal band anomaly. In several cases where there are band anomalies in the offspring a scute anomaly is found in the mother.

It has been shown clearly in several sets of offspring that there is an extremely close genetic relation between band anomalies and anomalies of single scutes. The two types of anomaly are merely more or less extensive expressions of the same genetic factor. Whenever a mother shows either type of anomaly, one or more offspring show one or the other type. The doubling factor is therefore strikingly dominant in the Mendelian sense. When we find sets of fetuses that show anomalies and the mothers of these show no anomalies, we must conclude that the anomaly is paternal, for a dominant factor in the mother, would appear phenotypically if present genotypically. It is interesting to note that almost the same number of sets have normal as have anomalous mothers.

Anomalous Offspring of Normal Mothers.

There are in the present collection 14 sets of fetuses showing band anomalies, the mothers of which showed neither band nor scute anomalies. In some ways these sets are better for our purposes than are those derived from anomalous mothers, because we can be sure of the uniparental character of the inheritance. Since the mothers show no anomalies, those in the offspring, being unquestionably inherited, must have come from the father. It would be highly interesting to know the conditions in the fathers, but the latter are inaccessible. Since there is no sex difference with regard to the anomalies, we may assume, however, that the same state of affairs would be revealed for the paternal as that made out for the maternal relation.

Some of the most interesting cases illustrating the symmetrical distribution of anomalies, intra- and inter-individually, are found among the offspring from normal mothers, and I shall give a complete tabulation of these sets, calling attention in the text only to certain of the more striking conditions, or to situations differing from those dealt with in the sets derived from anomalous mothers.

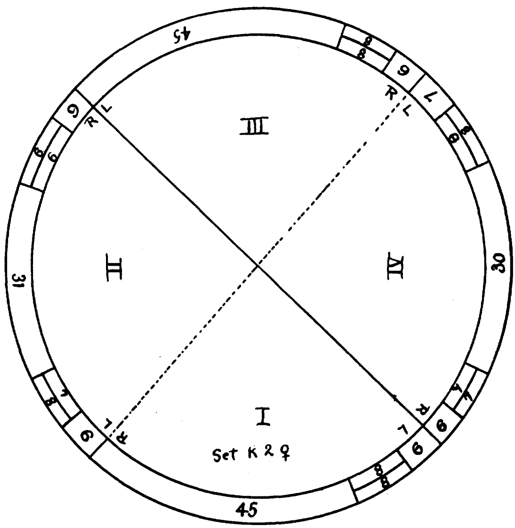
Set K. 2, ♀ *(Fig. 13).*

This set perhaps better than any other shows the phenomenon of symmetry reversal, or mirror-imaging among the quadruplets.

Fetuses I. and III., which face one another across the vesicle,

and are the secondary bud derivatives of II. and IV. respectively, are exact symmetrical reversals of each other, I. having the anomaly only on the left and III. only on the right.

Fetuses II. and IV., the two primary bud individuals, both show the anomaly bilaterally, but are also reversals, in that II. has the more extensive doubling 9–9 on the right and IV. has the



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more extensive doubling 9–8 on the left. It is interesting to note that the primary individuals II. and IV. are bilateral in their expression of the anomaly, and that the secondary individuals I. and III. are unilateral.

Set A. 64, ♂ (Fig. 14).

This set is remarkable for the striking identity of detail exhibited by the anomalies of the different fetuses.

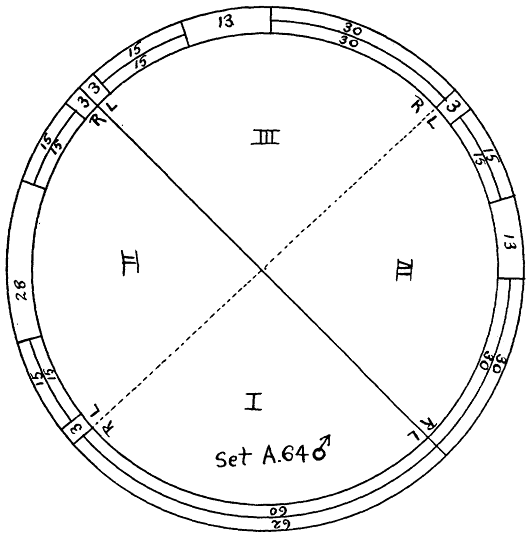
Fetus I. has both halves of band 1 completely double.

Fetus II. has both halves partially double and exactly bilaterally symmetrical, the doubling starting 3 scutes from the margin on each side and extending for 15–15 scutes.

Fetuses III. and IV are both exactly like II. on the left side and exactly like I. on the right.

There is exactly the same amount of doubling in I. plus II.

as there is in III. plus IV., but the distribution of the fully doubled and incompletely doubled half bands is different. In the case of the left-hand pair I. and II., I. gets both completely doubled halves and II. gets both incompletely doubled halves;



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while in the case of III. and IV. both get a completely and an incompletely doubled half. There is no symmetry reversal in this set.

Set A. 96, ♂ (Fig. 15).

Fetus I. has band 1 double except for 5 single scutes on the right margin.

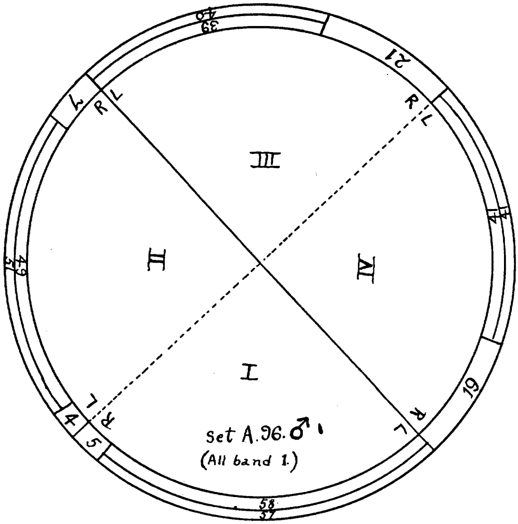
Fetus II. has a similar anomaly bilaterally.

Fetuses III. and IV. are very much alike but differ from I. and II. in the extent of the single part of the band, which is much longer than in the other pair. The pairing of fetuses is very clear, but no symmetry reversal is shown. One of four fetuses (II.) is bilateral.

Set K. 80, ♂ (Fig. 16).

Fetuses I. and II. are practically identical. In both band 1 is doubled, except for four single scutes on the left.

Fetuses III. and IV. show the incomplete doubling bilaterally



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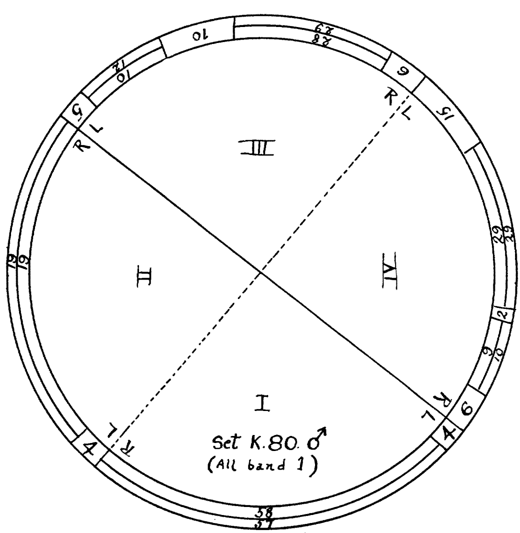

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with a larger and smaller series of double scutes arranged on opposite sides. Fetus III. has the long series 28–29 six scutes from the right, while fetus IV. has a series of 29–29 scutes 15 scutes from the left and extending past the middle. This is an imperfect reversal of symmetry. There is a better reversal in connection with the short series of double scutes, for in III. the series of 10–12 scutes is situated 5 scutes from the left, and in IV. the series of 9–10 scutes is situated 6 scutes from the right.

Set A. 101 (Table B2) has the anomaly confined to one pair of fetuses (I. and II.) and the expression is very different in the two. It is well to note that although the doubling is nearly complete in II. it starts after 6 single scutes at the margin, as is the case on both sides of I., which shows a remarkably exact bilateral symmetry.

In the remaining sets, K. 8, K. 12, C. 90, C. 63, C. 69, C. 72, C. 88, C. 32 and C. 41 (Table B2 and 3), band doubling is found in only one fetus of a set. In most sets however scute anomalies, which are usually rather definitely related to the band anomaly, are present in one or more fetuses. Set K. 8 is remarkable for the large amount of reduplication down the axis of scute anomalies, for example fetus III. has double scutes in bands 1, 3, 5, 7, and 8, those on bands 5 and 7 being reversals of each other. It is clear that all of the double scutes are in the same region of the band as is the double series in fetus I., and the majority are on the same side of the body.

The remaining sets show nothing that has not already been seen in sets previously described.

Summary and Conclusions.

Band anomalies are of the nature of irregularities in the normal regular rows of scutes that make up the typical band, and consist of more or less extensive regional doubling of rows of scutes in a band. This condition is typical for the non-banded parts of the armor but quite rare in the banded regions. It is practically confined to the band or bands nearest the non-banded region. Band anomalies occur in only about three per cent. of individuals and an examination of over two thousand adult individuals taken at random shows no duplicate anomalies.

These anomalies are strongly inherited but are subject to more or less modification. Sometimes a band anomaly unilaterally placed may be inherited unilaterally but with a reversed symmetry to that of the mother, or it may be bilateral. Sometimes an extensive doubling is inherited both as a similar band doubling, and as a single double scute in the individuals of a single polyembryonic set of offspring. Contrariwise a double scute in the mother may be inherited as a more or less extensive unilateral or bilateral band doubling. The peculiarity may also be reduplicated down the primary axis in two or more bands.

Frequently in unilateral anomalies the different fetuses of a set show reversed symmetry or mirror-imaging, but it is even more common to find the unilateral anomaly on the same side of most of the individuals, or bilaterally in one or more of them.

In a number of cases the anomalies in different fetuses of a set are so strikingly identical as to indicate a rigid predetermination of the details of the character, but in other cases there appears to be only a predetermination of a generalized anomaly that expresses itself to a greater or less extent in the various embryos. In terms of Mendelian inheritance we may say that an anomaly factor is inherited as a dominant character, but its distribution among the fetuses of a set and its location and extent are due to varying ontogenetic or epigenetic factors.

The distribution of these inherited anomalies among the various fetuses of the sets furnishes much interesting data, which, together with data on the inheritance of double scutes, to be presented subsequently, furnishes the basis of a discussion of several general questions and especially those involved in the concept of organic symmetry.

This subject is reserved for a subsequent paper of the present series.

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